PRELIMINARY OBSERVATIONS UPON THE BRAIN OF MENOPOMA.

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This is the second of a series of papers[1] upon the brains of the American Urodela. In the study of *Menopoma*, I have detected numerous errors in the first paper upon *Amphiuma*,[2] and my attention has kindly been called to others by Prof. Wilder and Dr. E. C. Spitzka.

The brains of *Amphiuma* and *Menopoma* are even more alike in their internal than in their external structure; while the reverse is the case in the comparison of *Menopoma* and *Menobranchus*, which resemble each other very closely externally, but in longitudinal section present important differences.

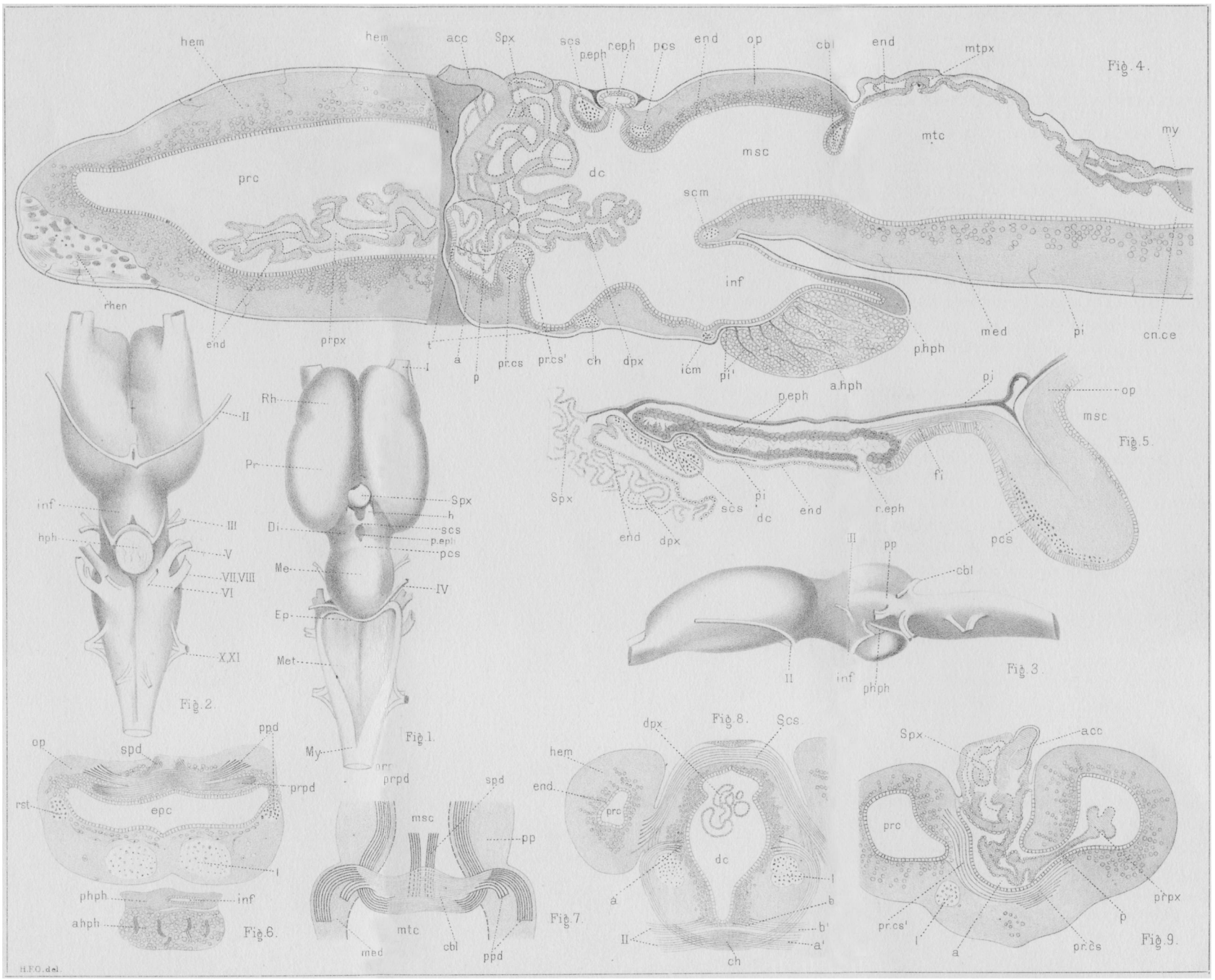
The greater accuracy of the Menopoma work is due to changes in technical methods. Before hardening, the brains were inflated with Müller's fluid, so as to preserve the natural proportion of the cavities. After treatment with alcohol, they were placed for a week in dilute carmine. Calberla's egg-mass was employed as before, except that the ventricles were injected with the mass before hardening. The delicate parts of the brain-roof were thus retained. It appears now that celloidin may be used for this purpose to equal, if not to greater, advantage in results, and with considerable economy of time. The sections were cut in absolute alcohol, were then floated upon a slide in consecutive order, from twenty to fifty at a time, and were covered with a delicate slip of blotting-paper during treatment with oil of cloves. These changes greatly improved the three series, which were obtained in as many planes—horizontal, transverse and vertical to the long axis of the brain.

External Structure (Pl. VI, figs. 1, 2, 3).

With a single exception, and that an important one, the brain of *Menopoma* approaches closely the typical brain. The seg-

[1] Many of these results were presented in the Biological Section of the American Association, September, 1884.

[2] Preliminary Observations upon the Brain of Amphiuma. Proc. Phila. Acad. Nat. Sc., July, 1883.



BRAIN OF MENOPOMA.

mental[1] parts are clearly differentiated from each other in regular succession, beginning with the olfactory lobes or Rhinencephalon, the Prosencephalon, the Diencephalon, the Mesencephalon, the Epencephalon and Metencephalon. This was not found to be the case in *Amphiuma*, where the Rhinen- and Prosencephala and Dien- and Mesencephala are barely distinguishable. The exception above noted is that, the epiphysis does not appear upon the external surface, but, as we shall see, is altogether wanting, while a vascular plexus lying between the hemispheres offers a very deceptive imitation of this important structure. The hypophysis and infundibulum, however, have a striking development.

A careful study of the surface of the diencephalon discloses a minute transparent area lying between two whitish streaks. The latter are transverse commissures in the roof of the third ventricle; the former is the cavity of the epiphysial tube, or recessus pinealis, the brain-cavity being separated from the pia mater only by a single layer of cells. This transparent area has already been pointed out by Goette[2] in the frog, where it is somewhat less conspicuous. In front of the foremost commissure is a triangular transparent space; at the sides of this are two horn-like forward continuations of the diencephalon. These processes I consider homologous with the habenulæ of the mammalian brain, and with the "Schnabelförmiger Fortsatz" described by Müller in the lamprey's brain. In the lamprey they coalesce in

[1] The nomenclature proposed by Prof. Burt G. Wilder has been adopted, with few exceptions. It proceeds upon the consistent plan of naming the segments, and their various parts, as far as possible, after the segmental names which now meet with general acceptance among anatomists; also of using abbreviated forms of the longer terms now in use. For the sake of clearness the new terms, and their synonyms, which are employed in this paper are given below. The *Prosencephalon*, including: the *procœliæ*, lateral ventricles; the *proplexi*, lateral plexuses; the *prosocœlia*, ventriculus communis laborum; the *supraplexus*, plexus in the roof of the prosocœlia; the *porta*, foramen of Munro; the *terma*, lamina terminalis; the *præcommissura*, anterior commissure. The *Diencephalon*, including: the *supracommissura*, commissura habenarum; the *processus* and *recessus pinealis*, the *postcommissura*, posterior commissure; the *diacœlia*, third ventricle. The *Mesencephalon*, including: the *mesocœlia*, iter, etc. A system of this kind must undergo modification, from time to time, but in the end it will be far superior to the present cumbersome multinomial system.

[2] Entwickelungsgeschichte der Unke, 1875.

the median line, but here they are separate, as may be seen by a close external examination, and verified by transverse sections. This homology is confirmed by the study of the foremost of the transverse commissures. In front of this space rises the reddish body, which has been generally mistaken for the epiphysis. In the natural state this body is not very prominent, but as soon as the ventricles collapse, it is thrust conspicuously upwards. The ventricular collapse is also the occasion of an artificial dorsal furrow in the optic lobe, which is here absolutely unpaired. Upon the ventral aspect of the brain we again observe two transparent areas. One resembles a long slit in front of the optic chiasma, and is found to be a portion of the lamina terminalis. The other is due to a thinning of the floor of the infundibulum, and is seen immediately in front of the hypophysis. The hemispheres are closely applied to each other, but have no structural union. The cerebellum is slightly overhung by the optic lobe.

The proportions of the various segmental parts are very similar to those of *Menobranchus*, and this seems to accord with the similarity of the proportions in the head, body and limbs of these animals.

Internal Structure.

A natural introduction to the internal structure would be a description of the walls and cavities of the various segments, but it happens that the boundaries of these segments can only be determined after we settle upon the relations of the parts which compose them, so, until some of the details have been investigated, this description must be postponed. In general, the brain is a tube forking in front into the paired lobes and cavities of the hemispheres.

The Ependyma and Pia Mater.—The pia mater closely invests all the brain surfaces and sends numerous nutrient vessels into its walls. It envelops all parts of the brain, with the exception of the hypophysis, which lies external to it (fig. 4), so that the pia actually separates the hypophysis from the floor of the infundibulum and sends in numerous smaller vessels between the epithelial tubes which constitute this body. This relation is not true of the posterior lobe of the hypophysis which is a development of the brain-wall and is surrounded by the pia, the anterior lobe as is well known, arising from the oral epithelium.

At several points the pia and ependyma unite to form the sole elements of the brain-wall, giving the transparent effect, in external view, which has been mentioned. A striking instance of this is seen in the dorsal wall of the infundibular cavity, which is extremely delicate, the ependyma consisting of a single row of cells. The vascular plexuses above the medulla and between the hemispheres are instances of such union, elaborated by the introduction of vascular plexuses from the pia. Three varieties of the cells of the ependyma can be distinguished. The cells of the first variety form a general investment of the inner brain-wall; they are from one to three deep, cylindrical or much elongated, crowded between them are yellowish oily granules, and many of the cells remotely resemble ordinary fat cells in the possession of a proto-plasmic nucleated centre, lying between yellowish, unstained terminations. It is the innermost of these cells which give rise to thread-like processes which radiate outwards in the brain-wall, but the latter never make such beautiful displays as are seen in the frog's brain, and figured by Stieda.[1] The cells of the second variety lack the fatty granules; they are found coating the *præcommissura*, but are principally observed wherever the brain-wall is reduced to a single row of cells as in the roof of the infundibulum, and in that part of the floor to which the hypophysis is attached; they are small, rounded cells, at one point becoming very much elongated, namely, in the sides of the *processus pinealis*. The transition from this to the third variety is beautifully shown in the forward portion of the roof of the third ventricle. Here the rounded passes into the beaded character of the single cell layer which follows the elaborate foldings of the *diaplexus*.

The consecutive series of sections in three planes afford fine material for the study of the nerve-fibre courses, and much has already been ascertained that throws light upon the relations of the brain segments. I will here describe only the fibre courses which have a transverse direction, considering under this head the relations of the cerebellum,[2] the origin of the optic nerves, and the various commissures.

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[1] Zeitschrift für wiss. Zool., Band xx.

[2] Compare E. C. Spitzka. The relations of the Cerebellum, Alienist and Neurologist. New York, January, 1884.

The Cerebellum (figs. 6, 7).—Numerous as are the errors which at present prevail in the literature of the amphibian brain, none are more striking than those relating to the cerebellum.[1] It is said to retain its embryonic condition of a small band-like structure stretching over the fourth ventricle. Now it happens that the amphibian cerebellum is a flat structure, and if viewed on edge, as is the case in looking down upon the frog's brain, it does appear very small; if, on the other hand, it is seen in vertical longitudinal section, its large bulk, relatively to other parts, is at once apparent. If, further, as will be done in another paper, a corresponding section of an amphiuma brain be superposed upon the frog section, we find that the former barely covers one-twenty-fourth of the diameter of the latter, although the Amphiuma is a very much larger animal. The description referred to above, then, is as exaggerated when applied to the frog as it is true of such forms as *Amphiuma*, *Menopoma* and *Menobranchus*.

In *Amphiuma*, the cerebellum is reduced to its simplest possible expression. It seems doubtful whether it contains any nerve cells whatever. In *Menopoma*, however, a few cells similar to those in the optic lobes, can be observed on either side of the transverse fibres which make up the larger part of this body; it is difficult to distinguish these cells from those of the ependyma. Notwithstanding the character of this body, its main relations to the adjoining parts are precisely similar to those of the higher vertebrates. These relations have already been indefinitely indicated by Stieda. (1.) From the lateral tips of the medulla arises a column of fibres on either side, which arches forward; here the columns are reinforced by fibres apparently arising from lateral cell-masses, these columns turn back and enter the cerebellum. (2.) Passing beneath these columns is another pair, which diverge and then converge as they enter the pars peduncularis of the mesencephalon; they can be followed some distance forwards upon either side of the mesocœlia. (3.) Passing directly forward from the ventral surface of the cerebellum, a few scattering fibres enter the valvula and with some doubt can be followed into the cells of the roof of the optic lobe. In one and two we recognize the post- and præ-pedunculi or inferior

[1] Mihalkovics, *loc. cit.*, p. 56; also, Wiedersheim, Lehrbuch der Vergleichenden Anatomie, 1883, p. 297.

and superior (processus ad cerebrum) peduncles of the higher vertebrate brain.

The scarcity, if not absence, of nerve cells in the Amphiuma or Menopoma cerebellum, renders it difficult to understand the meaning of these peduncles, unless we regard the cerebellum here as in large part a decussational system, composed of fibres crossing from one side of the brain to the other. It may be added that the frog's cerebellum is richly cellular.

The Optic Nerves (fig. 8).—No fibres have as yet been followed from the optic lobe (Mesencephalon) to enter the optic tracts, although there can be little doubt that they are present; but the fibres in the thalami arise in a manner which points, almost with certainty, to the important fact that in the Amphibia the *decussation of the optic tracts is incomplete.* In other words, part of the fibres of each optic nerve enter from the chiasma, *i. e.*, from the opposite side of the brain, part enter from the same side of the brain. (1.) The fibres supplying the chiasma, arise from cell masses in the upper lateral portions of the thalami, and sweep around the sides of the thalami, partly encircling the main longitudinal fibre system (crura cerebri); they pass downwards and obliquely forwards, enter the chiasma, and apparently pass to the nerve of the opposite side. (2.) In the floor and lower lateral cell masses of the thalami arise smaller bundles of fibres, which pass beneath the longitudinal system, above and then in front of the chiasma to enter the optic nerve of the same side. They can be traced by following successive sections forwards, but do not interdigitate with the fibres of the chiasma, as in the figure which combines the results of a series of sections. If this fact is confirmed by other observers, it will show that the partial decussation of the optic tracts is an early, if not a primitive condition, instead of being peculiar to the higher mammals, as has been generally maintained.

The Commissures.

The Præcommissura (fig. 9).—In the frog's brain [1] it has been found that there are two divisions of this commissure: a posterior, connecting the lower portions of the hemispheres, and an anterior, connecting the upper median walls. Both have been found in *Menopoma*, the latter arching upwards at the sides, and, as is clear in fig. 4, it forms on either side the posterior boundary of

[1] Stieda, *loc. cit.*, p. 308.

the porta, or passage from the single to the lateral cavities of the Prosencephalon. In *Menopoma*, however, the posterior division is immediately below the anterior, and it is found in the horizontal sections to be not a true commissural, but a decussational system. At this point, a large number of the fibres composing each of the longitudinal tracts, just mentioned in connection with the optic chiasma, cross each other and pass to or from the base of the opposite hemisphere. In *Menobranchus* these two tracts are completely separated, the upper division passing independently across the ventricle.

The Postcommissura.—Although this commissure is part of a conspicuous fold of the brain-roof separating the Dien- from the Mesencephalon, it really contains in the Amphibia but few fibres. Another interesting fact is that these fibres do not enter into the thalami, but pass obliquely backwards into the region of the longitudinal tracts composing the pars peduncularis of the Mesencephalon. This accords with Mihalkovics'[1] observations upon the chick, and tends to confirm Pawlowsky's[2] view that this is not a commissure in the strict application of the word, but is rather a side connection of the longitudinal fibre system. This view accords also with Ahlborn's recent observations upon the lamprey.

The Supracommissura (fig. 8).—In the forward portion of the roof of the diacœlia, and immediately above the optic chiasma is a commissure, which, as far as I can ascertain, has been heretofore entirely overlooked in the Amphibia. In *Menopoma* and *Amphiuma* it is very large; in the frog it is much reduced, and lies further forward; in *Menobranchus* it is represented by a slender band of fibres immediately in front of the *recessus pinealis*. In all these forms it lies in front of the epiphysial process, and completely separates this tube from the dia- and supraplexus. It occupies the same relative position as the variously named *Commissura habenarum*,[3] or the commissure of the pineal stalk (Mihalkovics)[4] of the mammalian brain, as well

[1] *Loc. cit.*, p. 73.

[2] Pawlowsky, Ueber den Faserverlauf in der hinteren Gehirncommissur. Zeits. für wiss. Zool., Band xxiv, 1874.

[3] Wilder, Anatomical Technology, 1882, p. 452.

[4] *Loc. cit.*, p. 100. This comparison is somewhat doubtful.

as the commissure figured by Professor Balfour[1] in the Elasmobranch brain. It passes across the posterior ends of the hook-like processes of the thalami, which I have compared with the habenulæ, and the most satisfactory interpretation of this commissure is afforded by a comparison with Ahlborn's figures of the lamprey brain.[2] At the sides and to the front of the *recessus pinealis*, I find in *Menopoma* two compact masses of nerve cells, which I think we may compare with the *ganglia habenarum*. These masses form the posterior, and to some extent the inferior, boundary of the *supracommissura*. Following the fibres of this commissure downwards and forwards, we find that they partly enter the thalami, while the greater part pass directly into the hemispheres. Their distribution, then, is similar to that of the fibres of the *tænia thalami optici*, while the commissural portion may be compared with a slender commissure, the *commissura tenuissima*, traversing the habenulæ in the lamprey's brain. The relations to the hemispheres are especially interesting, as they indicate, between the posterior parts of these bodies, a commissural union of considerable extent and importance.

Infundibular Commissures.—The lobes of the infundibulum are united dorsally and ventrally by two commissures, the uppermost being quite distinct and extensive (fig. 4) and forming the thin fold which divides the iter from the infundibular cavity.

The Hypophysis and Epiphysis.

The backward extension of the *hypophysis*, together with its great development, and the unusual size of the infundibular cavity and lateral lobes, lend this portion of the brain especial interest. I will, however, only remark here upon the clear separation of the anterior and posterior lobes of the hypophysis, by the turning in of the pia mater over the forward face of the anterior lobe (fig. 4). The vessels of the pia ramify between the columnar epithelial cells, which compose the tubes forming this lobe. In vertical section the lumen of one of these tubes is occasionally seen. The ependyma is much convoluted in the posterior lobe, and these foldings may readily be mistaken for tubes.

Our knowledge of the *epiphysis* in the Amphibia is in a far from satisfactory state. There can be little doubt as to the correctness

[1] Elasmobranch Fishes, plate xv.

[2] *Loc. cit.*, p. 285.

of Goette's important observation[1] that in the batrachia the epiphysis proper loses its primitive connection with the brain, and lies external to the skull, while its primitive union with the brain is indicated by the more or less degenerate walls of the epiphysial tube. Yet Goette's figures do not give such a clear history of these changes, as the importance of the subject demands, and so far as we know, there have been no embryological investigations on this subject among the urodela.

In the meantime, since the publication of Goette's discovery, many general works[2] by different writers upon comparative anatomy have appeared, all of which figure the epiphysis as a conspicuous object lying between the cerebral hemispheres. There can be little doubt that these, as well as all the earlier writers upon the Amphibian brain, such as Wyman, Ecker, Leidig, Rathke and Stieda have mistaken the remarkable upgrowth of the vascular plexus above the prosocœlia for the epiphysis, and that this body in the urodela, as well as in the batrachia, is represented upon the brain surface merely by a portion of its primitive stalk. The grounds for this statement, so far as it concerns the urodela, are that in *Amphiuma*, *Menobranchus* and *Menopoma* portions of this primitive stalk can be seen in vertical section, in different stages of arrest, and retaining to a greater or less extent the primitive condition of a glovefinger-like upfolding of the brain roof.

In the discovery of the supracommissura and the invariable position of the recessus pinealis, between this and the post-commissura, we find unmistakable anatomical evidence for Goette's conclusions, although we are not thereby warranted in assuming that the development of the epiphysis is the same in the urodela as in the batrachia. All doubt is also removed as to the connection between the stalk of the epiphysis and the supraplexus, as the latter is clearly distinct from the former, and does not establish such close relations with the stalk as in the birds.

In *Menopoma* (fig. 4) the ependyma cells upon either side of the recessus become much enlarged and elongated; upon the upper surface of the brain they lose this character, becoming

[1] Entwickelungsgeschichte der Unke, 1875, p. 283.

[2] Huxley and Martin's Practical Biology, Wiedersheim's Lehrbuch der vergleichenden Anatomie and Wilder's Anatomical Technology may be cited as examples.

small and spherical, and folding over, form a single-layered much flattened sac, the lumen of which retains its connection with the diacœlia by a narrow slit. This is the only adult trace of the *processus pinealis* in *Menopoma*. In *Rana* (fig. 5) I find the same elongation of the ependyma cells, and similar cells forming the processus, but in a double row. Here the supracommissura is much smaller, and more widely separated from the postcommissura, this interval is bridged by a delicate single row of cells which appear to turn up and form the anterior border of the recessus, although this point is not very clear. There is also some doubt whether the lumen of the processus retains its communication with the diacœlia. The processus itself is a long, flattened, two-layered sac, circular in section, extending anteriorly so as to overlap the supracommissura. The pia mater overlaps the processus upon all sides, indicating that it primitively was directed upwards. Extending from above the *postcommissura*, forwards to the base of the epiphysial stalk, are numerous fibres, which appear to enter into relations with the cells of the stalk. In *Menobranchus* and *Amphiuma* we find a nearer approach to the frog than to the *Menopoma* condition, the processus forming an elongated flattened sac, completely constricted off from the brain cavity.

The Plexi choroidei.—There is a singularly simple and beautiful display of the relations of the intra-ventricular blood-vessels in the brain of *Menopoma* (fig. 4). The thrusting in of the ependyma extends from the supracommissura to the upper portion of the terma. The arterial supply is apparently derived from the median arteria carotis cerebralis, and the venous return is at the sides of the supraplexus. The division into supra-, dia- and proplexus is a somewhat artificial one here, but is not so when applied to the Amphiuma brain, where the supraplexus is very prominent, and the diaplexus extends well back into the Mesencephalon. The lateral wings of the diaplexus are shown passing through the porta in fig. 9. The nature of the ependyma cell-lining of these vessels is very constant; small and large, the cells have the same elongated, bead-like appearance.

The Encephalic Segments.—Stieda,[1] following general usage, considers that portion of the median brain-floor lying behind the

[1] *Loc. cit.*

chiasma as the lamina cinerea; that lying in front, as the lamina terminalis. This construction cannot be applied here with accuracy, owing to the unusual position of the *præcommissura*, in the brain-floor, instead of in the anterior median wall. Yet for comparative purposes it is best to retain this interpretation. It gives us an unusually extended prosocœlia, or ventriculus communis loborum, which we find is a distinctive feature also of the Amphiuma and Menobranchus brain. The *supracommissura* may be considered as the upper posterior boundary of the prosocœlia, separating it arbitrarily from the diacœlia, as the *postcommissura* does the dia- from the mesocœlia. At all events, the supraplexus clearly belongs to this cavity rather than to the diacœlia.

The general subject must be discontinued here, to be resumed in connection with the brain of the Menobranchus, in a subsequent paper.

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EXPLANATION OF PLATE VI.

ILLUSTRATING THE BRAINS OF MENOPOMA AND RANA.

Encephalic segments Rh.—Rhinencephalon; *Pr.*—Prosencephalon; *Di.*—Diencephalon; *Me.*—Mesencephalon; *Ep.*—Epencephalon; *Met.*—Metencephalon.

General Abbreviations.

a.—Prosocœlia, cavity of the primitive prosencephalon.
a. hph.—Anterior lobe of hypophysis.
a c c.—Branch of *Arteria carotis cerebralis.*
cbl.—Cerebellum.
ch.—Optic chiasma.
cn. ce.—Canalis centralis.
dc.—Diacœlia, third ventricle.
dpx.—Diaplexus, choroid plexus of the third ventricle.
end.—Ependyma.
h.—Habenulæ.
hem. and *hem'.*—Section and external surface of right hemisphere.
hph.—Hypophysis.
i. cm.—Inferior commissure of infundibulum.
l.—Longitudinal fibre courses, cut transversely.
med.—Medulla oblongata.
msc.—Mesocœlia, iter.
mtc.—Metacœlia, fourth ventricle,
mtpx.—Metaplexus, *tela vasculosa* of the fourth ventricle.
my.—Myelon, spinal cord.

opt.—Optic lobe.
p.—Porta, Foramen of Munro.
pcs.—Postcommissura, posterior commissure.
p. hph.—Posterior lobe of hypophysis.
pi.—Pia, pia mater.
ppd.—Post-pedunculus, posterior peduncle of cerebellum.
pp.—Pars peduncularis of Mesencephalon.
prc.—Procœlia, lateral ventricle.
pr. cs. and *pr. cs'.*—Præcommissura, anterior commissure, lower and upper divisions.
pr. eph.—Processus pinealis, the epiphysial stalk.
pr. px.—Proplexus, the choroid plexus of the lateral ventricle.
pr. pd.—Præpedunculus, anterior peduncle of cerebellum.
r. eph.—Recessus infra-pinealis, the opening of the epiphysial cavity into the diacœlia.
rhen.—Section of olfactory lobe.
rst.—Restiform tract.
scs.—Supracommissura, commissure of the habenulæ.
scm.—Superior commissure of the infundibulum.
spx.—Supraplexus (formerly considered the epiphysis), the upper portion of the vascular plexus of the prosocœlia.
spd.—Supra-pedunculus, fibres passing from the cerebellum into the optic lobe.
t.—Terma, lamina terminalis.

FIGURES 1, 2, 3. Dorsal, ventral and lateral aspects of the brain of *Menopoma Alleghense*, enlarged five diameters. The whitish band stretching across the infundibulum, in front of the hypophysis, probably consists of the inferior infundibular commissure. In the dorsal aspect of the fresh brain, the position of the epiphysial process, is marked by an oval transparent area, in front and behind which, the supra- and post-commissuræ shine through. This area is undoubtedly contracted by reagents. The natural backward direction of the cerebellum is also altered, so that it hangs beneath the optic lobe.

FIGURE 4. Longitudinal vertical section of the brain of Menopoma, in a median plane as far forwards as the terma, and in front of this through the centre of the right hemisphere; enlarged sixteen diameters. The dotted ellipse indicates the position of the porta, or foramen of Munro.

FIGURE 5. The diatela, or roof of the third ventricle of the brain of *Rana Mugiens*. This figure represents the long tubular epiphysial process, composed of two or three rows of cells, mostly enveloped by the pia and extending forwards above the supracommissura. The inner layer cells send short processes into the persistent cavity of the epiphysis, and the cavity is filled by a highly transparent meshwork, which may simply consist of coagulated fluid. The opening into the diacœlia, *r. eph.*, is doubtful. The lines (*fi.*), indicate a number of nerve fibres, which apparently extend to the base of the epiphysial process.

FIGURES 6–9 are of *Menopoma*.

FIGURE 6. A composite of three transverse sections through the cerebellum and medulla.

FIGURE 7. Diagrammatic representation of the nerve fibre courses springing from the cerebellum.

FIGURE 8. A composite of six sections through the diencephalon, showing the course of the fibres of the supracommissura, and probable origin of the optic tracts. *a*–*a'*, supposed course of fibres passing from upper parts of thalamus to optic nerve of opposite side. *b*–*b'*, course of fibres from lower parts of thalamus to optic nerve of same side.

FIGURE 9. An oblique section through the region of the præcommissura, showing the distributions of the fibres of this commissure, also the supraplexus, the proplexus, and porta. The right side is cut anterior to the left.